Effects of social interaction on the electric organ discharge in a mormyrid fish, *Gnathonemus petersii* (Mormyridae, Teleostei)

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Summary

African weakly discharging electric fish (Mormyridae) use their self-generated electric signals and electroreceptive abilities for orientation and communication in the context of courtship and territorial interactions. This paper documents socially mediated changes in the electric organ discharge (EOD) of subadult *Gnathonemus petersii* under non-breeding environmental conditions. Increases in EOD duration and changes in the relative phase amplitudes occurred in dominant fish during same-sex (male–male, female–female) and opposite-sex interactions. Similar changes were also observed in fish that were restricted in their physical interactions, suggesting that direct contact is not necessary to induce dominance-typical EOD waveforms. The possible communicative functions of these changes are discussed.

Key words: Mormyridae, *Gnathonemus*, social behavior, electric organ discharge, behavioral plasticity.

Introduction

African weakly discharging electric fish (family Mormyridae) use their self-generated electric signals [electric organ discharges (EODs)] and their electroreceptive abilities for orientation and communication (Hopkins, 1986; Moller, 1995; von der Emde, 1998; Rojas and Moller, 2002). EODs play a major role in territorial interactions (Kramer and Bauer, 1976; Crockett, 1986; Kramer, 1990). The waveform of the EOD does not vary appreciably over short time periods and thus potentially communicates the individual's identity such as sex, species (Hopkins and Bass, 1981; Hopkins, 1983, 1986, 1988) and developmental state (Westby and Kirschbaum, 1977, 1978; Kirschbaum, 1987, 1995). Several species generate sexually dimorphic EODs, with mature males typically emitting longer EODs than females (e.g. Hopkins, 1980, 1981, 1986; Westby and Kirschbaum, 1982; Bass, 1986; Landsman, 1993a,b). Sexually immature males possess short, female-like EODs.

There are, however, a number of factors that can influence the EOD in the short term, including environmental conditions such as water temperature and conductivity (reviewed by Moller, 1995) as well as biological factors such as a male's position in the dominance hierarchy (Carlson et al., 2000). Increases in EOD duration comparable with those observed in dominant fish also occur following androgen treatment (Bass and Hopkins, 1985; Bass, 1986; Landsman and Moller, 1988; Landsman et al., 1990; Herfeld and Moller, 1998). South American gymnotiform electric fish also show fluctuations in both EOD amplitude and duration (Hagedorn, 1995; Franchina

and Stoddard, 1998; Franchina et al., 2001). Social interaction affects the EOD rate (Dunlap, 2002; Dunlap et al., 2002) and duration (Franchina et al., 2001) of gymnotids, and increases in the EOD duration can be induced by androgens (Few and Zakon, 2001).

The current experiment was designed to test the hypothesis that subadult *Gnathonemus petersii* are capable of exhibiting socially mediated EOD changes outside the species' breeding season, i.e. in the absence of exogenous factors such as water conductivity and water level that trigger the cyclic reproductive conditions in mormyrid fish (Kirschbaum, 1995, 2000). The presence of such changes would suggest that EODs are involved in communication in the context of territorial and/or dominance interactions and are not restricted to mate attraction. To date, socially mediated changes in EOD duration and amplitude have not been reported under non-breeding conditions. The specific aims of this paper were (1) to ascertain whether the subadult mormyrid EOD is affected by social interactions in a manner comparable with that observed in adult fish, (2) to determine whether such changes differ between and within the sexes and (3) to compare the effects of free and restricted social interactions on the subadult EOD.

Materials and methods

Animals

Subjects were subadult *Gnathonemus petersii* Günther 1862, obtained through the aquarium trade (Aquarium Glaser,

Frankfurt, Germany): females, 137±2.2 mm (standard length), 22.1±1.1 g (mass); males, 140±3.3 mm, 19.7±1.6 g. Sex was determined from radiographs of all subjects followed by *post-mortem* gonadal inspection of a subset of these fish. Adult and subadult males show bone expansion at the base of a select number of anal fin rays (Brown et al., 1996; Pezzanite and Moller, 1998); this characteristic is lacking in females.

Apparatus

Fish were singly housed in 19-liter aquaria and kept under a 12 h:12 h L:D regimen with lights on at 07.00. The stimulus (interaction) tanks were 57-liter aquaria (length, 60 cm; width, 30 cm; water depth, 25 cm). Water conditions in both the holding and interaction tanks were held constant within limits (conductivity, 178±6.3 μS cm^{-1}; temperature, 24.9±0.2°C). To restrict fish in their interactions, a plastic mesh divider (0.75 cm thick; mesh squares, 1.5 cm×1.5 cm) was inserted into the tank, separating the interaction area into two equal compartments (Fig. 1). This partition allowed free water flow between compartments, thus permitting electric interaction but preventing the fish from direct physical contact. The opaque mesh also partially restricted vision and potential lateral-line-mediated cues.

EOD measurements

EODs were monitored with a pair of Ag/AgCl recording electrodes, placed at the head and tail region of each fish, pre-amplified and displayed on an oscilloscope (Hitachi digital storage, model VC-6023). The EOD of *G. petersii* consists of four phases, P1, P2, P3 and P4 (Fig. 2). We restricted our analysis to P2 and P3, the two phases exhibiting the largest positive and negative amplitudes, respectively. We will refer to the sum of P2 and P3 durations as EOD duration. P2 duration was measured from its initial positive-going zero crossing to the intersection with baseline. P3 duration was measured from the end of P2 to the ascending intersection with baseline. Peak amplitude measures were taken for P2 and P3. The amplitude ratio $A2/A3$ served as a derived variable. EOD duration and amplitude ratio were collected daily (during the fish's early subjective day). EOD duration is affected by temperature; therefore, data were adjusted to a conventional standard of 25°C using a calibration function based on a data set obtained from *G. petersii* (see Herfeld and Moller, 1998).

Interaction conditions

Fish were initially housed singly for 4 days and were subsequently placed into a tank with a neighbor for a 4-day interaction period. Following this period, they were returned to their home tanks for another 4 days. The social interaction varied in three ways.

(1) Free interaction (five male–male pairs, five female–female pairs and five male–female pairs). Each tank contained only one ceramic shelter tube, and there was no other possible 'hiding' place. Under daylight conditions, these fish prefer hiding in sheltered areas (Rojas and Moller, 2002). Dominant fish exclude subordinates from such shelters (Mack, unpublished, as cited in Moller, 1995, p. 248; Carlson et al., 2000). Here, we assigned dominance status to the fish that excluded its neighbor (subordinate) from the sole available shelter.

(2) Restricted interactions (five male–male pairs and five female–female pairs). Under this condition, fish were separated
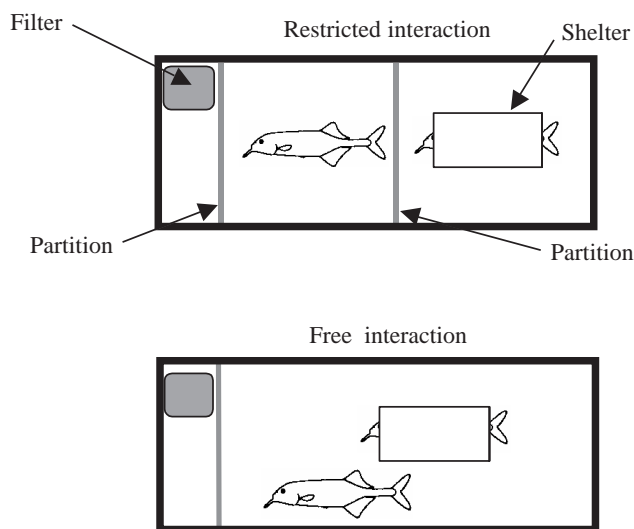

Fig. 1. Test tanks illustrating how fish were either restricted in their interactions (upper panel) or could freely interact (lower panel). The central divider consisted of a plastic mesh partition. Dividers on the left prevented fish from hiding behind the tank's filter.
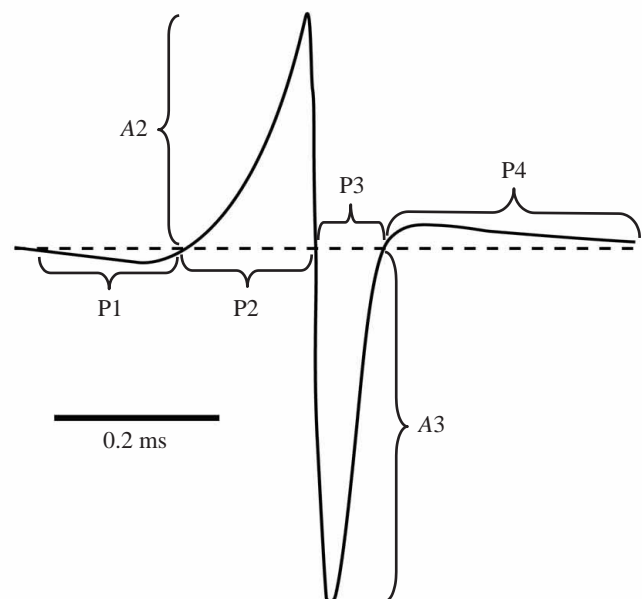

Fig. 2. A typical electric organ discharge (EOD) from a subadult *G. petersii*. EODs consist of four phases: P1, P2, P3 and P4. The combined durations of P2 and P3 were used as the duration measure in this study. $A2$ and $A3$ refer to the amplitudes of phases 2 and 3, respectively.

by the plastic mesh partition. One fish in each pair was randomly assigned access to a shelter. The second subject, isolated in the neighboring compartment, had no shelter access.

(3) Solitary control fish (five males and five females). Fish under this condition were singly housed in the same type of tank used for the other two conditions. One half of control subjects were randomly assigned access to a shelter during the 4-day sampling period and the other half had no shelter access.

Statistical procedures

Between-subjects analysis of variances (ANOVAs) were run with repeated measures within subjects (mixed-model ANOVAs). ANOVAs were performed using Statistica for Windows (Statsoft, Inc., Tulsa, OK, USA). The significance level was set at $P<0.05$. The dependent measures for different ANOVAs were EOD duration and $A2/A3$ amplitude ratio. The independent variables in different ANOVAs (depending on the group being tested) were interaction level, dominance status and sex. Separate ANOVAs were run for male–male and female–female pairs. The ANOVAs and the independent variables tested for each group are listed in the Results. Where applicable, Tukey's honest significant difference *post-hoc* tests were performed. Mean data for the three individual manipulation periods (days 1–4, pre-interaction; days 5–8, interaction; and days 9–12, post-interaction) were used as repeated measures in all ANOVAs.

Post-hoc comparisons of interaction effects (manipulation period × dominance status) were not possible, however. This was due to the fact that there was no clear choice of an appropriate error term for comparisons that involve between- and within-group interactions (Statistica for Windows program manual).

All procedures complied with local, state and federal regulations and were approved by the Hunter College Institutional Animal Care and Use Committee (protocol # PM/TT 6/03-02).

Results

Free interaction

EOD duration increased during the social interaction periods in male–male, female–female and mixed-sex pairs. Relative to subordinates and controls, increases only occurred in dominant fish (Fig. 3). The EOD duration in all three groups showed a significant difference within subjects (Table 1, ANOVAs 1, 3, 5). EOD duration increased during interaction in female–female pairs ($F_{2,24}=5.58$, $P<0.05$; Fig. 3A); a *post-hoc* analysis revealed that the EOD was significantly longer during the interaction (326.8 μs) than during the pre-interaction period (310.9 μs). A status-based difference between the EODs of female pairs was shown by a significant status × manipulation period interaction ($F_{4,24}=5.02$, $P<0.01$).

EOD duration also changed in males ($F_{2,24}=6.32$, $P<0.01$; Fig. 3B); there were significant differences between interaction (297.9 μs) and both the pre-interaction (308.8 μs) and post-
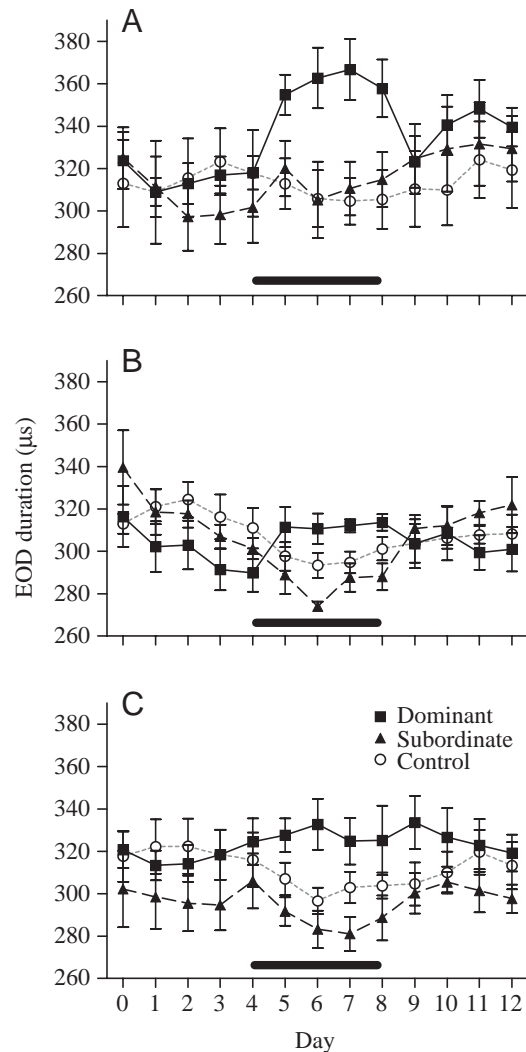

Fig. 3. Effect of dominance status on mean electric organ discharge (EOD) duration (error bars ± 1 s.e.m.) of freely interacting female–female (A), male–male (B) and mixed-sex (C) pairs of *Gnathonemus petersii* (*N*=5 fish per group). EOD duration increased in all groups during interaction, with most of the increase occurring in dominant fish. The horizontal bar spanning days 4–8 represents the duration of interaction.

interaction (308.6 μs) periods. These differences were due to a decrease in the EOD duration in subordinates and controls but not in dominant fish, as suggested by a status × manipulation period interaction ($F_{4,24}=9.13$, $P<0.0001$).

In different mixed-sex pairs, individuals of each sex established dominance. Of the five mixed-sex pairs, three possessed dominant males and two possessed dominant females. These pairs showed dominance-associated EOD differences similar to those in the same-sex dyads (Fig. 3C). EOD duration increased in dominants relative to subordinates, as shown by a significant dominance × manipulation period interaction (Table 1, ANOVA 5; $F=3.29$, $P<0.05$).

Amplitude ratios (Table 1, ANOVAs 2, 4) increased in male–male ($F_{2,24}=3.68$, $P<0.05$) and female–female

Table 1. *ANOVAs assessing dominance status*

| ANOVA # | Dependent variable | Independent variable | | Repeated measures (manipulation periods) |
		Sex	**Dominance status**	
1	Duration	F	**Dom/sub/alone**	**Pre, interaction, post**
2	Amplitude	F	**Dom/sub/alone**	**Pre, interaction, post**
3	Duration	M	**Dom/sub/alone**	**Pre, interaction, post**
4	Amplitude	M	**Dom/sub/alone**	**Pre, interaction, post**
5	Duration	**M+F**	**Dom/sub/alone**	**Pre, interaction, post**
6	Amplitude	**M+F**	**Dom/sub/alone**	**Pre, interaction, post**

Independent variables are indicated in bold. One independent variable was sex (in mixed-sex pairs only). The second independent variable (dominance status) had three levels: dom, dominant; sub, subordinate; alone, solitary. The dependent variables' 'amplitude' category is the amplitude ratio ($A2/A3$). Repeated measures categories: pre, pre-interaction period; interaction, social interaction period; post, post-interaction period.

($F_{2,24}=3.48$, $P<0.05$) pairs. In females, a *post-hoc* analysis revealed a significant difference between pre-interaction (0.649) and interaction (0.670) periods. In males, the amplitude ratios were higher during interaction (0.640) than during post-interaction (0.617). Dominant fish (i.e. that excluded their neighbors from access to the shelter) thus showed a trend of increased amplitude ratio during the interaction periods (Fig. 4A–C). These changes in amplitude ratio corresponded with increases in EOD duration. In mixed-sex pairs, however, the difference in amplitude ratios was not significant (Table 1, ANOVA 6).

Restricted interaction

During restricted interactions, fish could not make physical contact but were able to detect each other's EODs. We hypothesized that under such conditions the EOD would (1) not change in either fish, (2) assume dominant characteristics in one fish or (3) assume such characteristics in both. A comparison of EOD durations (under restricted and free conditions) showed a comparable increasing trend in female–female pairs (Fig. 5A) and no change in male–male pairs (Fig. 5B). The EOD in solitary fish of both sexes remained, as expected, unchanged.

There was a significant manipulation period effect upon EOD duration in both female–female ($F_{2,44}=8.25$, $P<0.001$) and male–male ($F_{2,44}=3.66$, $P<0.05$) pairs (Table 2, ANOVAs 1, 3). In females, EOD duration during the interaction (326.5 µs) and post-interaction (321.0 µs) periods was significantly longer than during pre-interaction (303.6 µs). The EOD duration in female–female pairs also showed a significant interaction between manipulation periods and the

free, restricted or solitary types of interaction ($F_{4,44}=3.73$, $P<0.05$; Table 2, ANOVA 1). Although *post-hoc* tests could not be performed on this interaction effect, Fig. 5A shows that during the interaction period the solitary group differed most
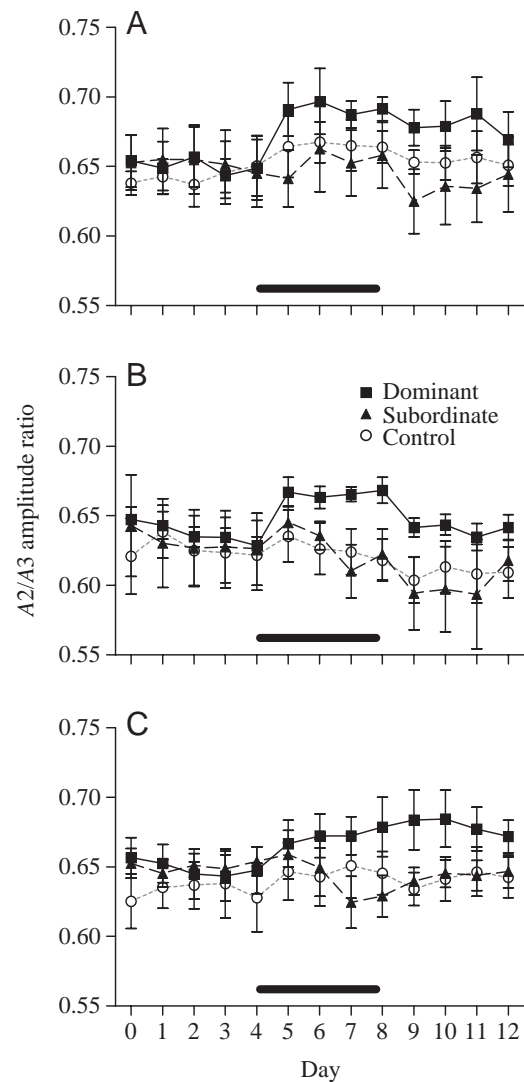

Fig. 4. Effect of dominance status on mean amplitude ratio (error bars ± 1 s.e.m.) of freely interacting female–female (A), male–male (B) and mixed-sex (C) pairs of *G. petersii* (*N*=5 fish per group). Amplitude ratios increased in male and female pairs, with the highest amplitude ratios occurring during interaction. Dominant fish showed a trend of increasing amplitude ratio across manipulation periods. The horizontal bar spanning days 4–8 represents the duration of interaction.

Table 2. *Interaction type ANOVA assignments*

ANOVA #	Dependent variable	Sex	Interaction type	Manipulation
1	Duration	F	**Free/restricted/solitary**	**Pre, interaction, post**
2	Amplitude	F	**Free/restricted/solitary**	**Pre, interaction, post**
3	Duration	M	**Free/restricted/solitary**	**Pre, interaction, post**
4	Amplitude	M	**Free/restricted/solitary**	**Pre, interaction, post**

All independent variables compared in a given ANOVA are indicated in bold. Groups include: free, freely interacting; restricted, restricted interaction; solitary, controls. Manipulation periods include: pre, pre-interaction; interaction, social interaction period; post, post-interaction period.

from the freely interacting and restricted groups. In male–male pairs, there was no difference in EOD duration between the different types of interaction (Fig. 5B) and there were no significant differences in amplitude ratios between any freely interacting, restricted and solitary groups (Table 2, ANOVAs 2, 4).

Dominant fish in freely interacting male–male and female–female groups showed no sex difference in EOD duration, although the differences in EOD duration did approach significance ($F_{1,24}=3.87$, $P=0.0609$). There was a significant sex difference in amplitude ratio between these groups ($F_{1,24}=4.72$, $P<0.05$). *Post-hoc* analysis of these data showed that females (0.658) had a significantly higher

amplitude ratio than males (0.629), but no significant interaction between sex and dominance status existed.

Discussion

The results demonstrate that changes in EOD duration and relative phase amplitudes may serve in communicating social status among subadults of either sex and that such changes are not restricted to the breeding season. The hormonal correlates presumably underlying EOD changes in subadults may relate to dominance signaling rather than mate attraction. Under breeding conditions, dominant males in mixed-sex groups of *Brienomyrus brachyistius* expressed androgen-associated EOD lengthening (Carlson et al., 2000). It is not known if dominant females would express similar changes under breeding conditions. Under non-breeding conditions, we have found such dominance-mediated EOD changes in both sexes.

Signaling dominance

Signaling dominance may be equally important for subadults of both sexes, particularly during the dry season as territories dry up and food supplies diminish. In many mormyrids, the EOD sex difference is prominent only during the breeding season (Hopkins, 1981; Landsman, 1993a). This difference, as Carlson et al. (2000) have shown, can be further enhanced (in males) during social/dominance interactions. During the breeding season, females may suppress dominance signaling in order to facilitate access to a male-defended territory. Thus, dominance signaling in female *G. petersii* should occur only prior to sexual maturity and/or during the non-breeding season. Our hypothesis predicts that the female EOD during breeding conditions will resist social and/or androgen-mediated changes, remaining consistently shorter and with less inter-individual variability than the EODs of males under similar conditions. This is indeed the case in other mormyrids such as *B. brachyistius* (Carlson et al., 2000) and *Mormyrus rume proboscirostris* (P. Moller, C. Schugardt and F. Kirschbaum, unpublished).

That subadult female mormyrids can respond to circulating androgens has been amply demonstrated in hormone administration studies, resulting in male-like changes in the EOD waveform (Bass and Hopkins, 1985; Landsman and Moller, 1988; Landsman, 1995; Herfeld and Moller, 1998). Such laboratory tests have always been conducted under
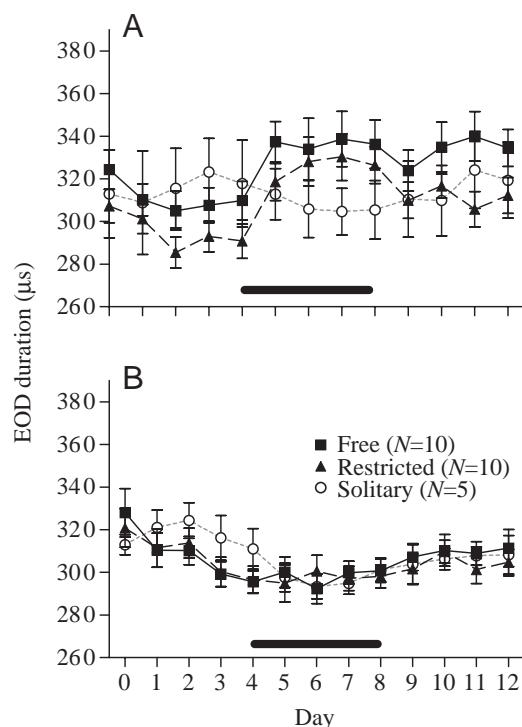
Fig. 5. Mean electric organ discharge (EOD) duration (error bars ± 1 S.E.M.) of freely interacting, restricted interaction and solitary female–female (A) and male–male (B) pairs of *G. petersii*. Both free and restricted female pairs showed a comparable increasing trend. This trend did not occur in male pairs. The EOD in solitary fish of both sexes remained unchanged. The horizontal bar spanning days 4–8 represents the duration of interaction.

carefully controlled environmental conditions, including relatively invariant water conductivity, mimicking aquatic conditions typical of the non-breeding season.

EODs as a status badge

The EOD changes resulting from social interaction may serve to differentiate individual status in groups. Differences in inter-individual EOD duration may serve as badges of current status, reducing unnecessary conflict. Many species of fish use coloration and markings to signal dominance, with high-ranking individuals taking on coloration (associated with hormonal condition) only as a result of social dominance (Magurran, 1986). Communication using status badges is well documented in birds (e.g. Harris sparrows *Zonotrichia querula*), where black feathers correlate with both testosterone and social dominance (Rohwer, 1975, 1982; Rohwer and Rohwer, 1978). The mormyrid EOD might serve as an electric badge, as EOD duration correlates with both androgens and social dominance in these fish.

Our data lend support to the hypotheses that in restricted

interactions there are either dominant-like changes in one fish (suggesting that dominant status is attained under restricted conditions) or that dominant-like EOD changes occur in both individuals (suggesting that changes that can occur in both members of a restricted pair are suppressed in subordinates only as a result of free interaction). During restricted interactions, we recorded dominant-like EOD changes in either one or both members of a female pair. To assess whether only one or both fish in an interacting dyad showed dominant-like changes, we reanalyzed the data collected from restricted female–female interactions (Fig. 6). Within-pair differences were used to designate members to one of two groups: pseudo-dominant or pseudo-subordinate. Individuals that showed a larger increase in EOD duration relative to their neighbor at the onset of restricted interaction were designated as pseudo-dominant. The neighbors of these pseudo-dominant individuals were assigned to pseudo-subordinate status (it was not possible to perform parametric statistical analyses on these data, as group assignment was based upon EOD measures). Without exception, freely interacting dominant females (see Fig. 3A), like pseudo-dominant females, showed increases in EOD duration relative to their neighbors. In both pseudo-dominant and pseudo-subordinate groups, we noted an increasing trend in EOD duration during interaction (Fig. 6A).

In the pseudo-subordinate fish, there was no increase in amplitude ratio during the interaction period, although amplitude ratio in this group did remain higher than or comparable with that of the pseudo-dominant group throughout this period (Fig. 6B). The possibility that pseudo-dominant restricted fish would also show dominant status in free interaction was not tested.

The EOD duration of dominant females and males (Fig. 3A and Fig. 3B, respectively) and both pseudo-dominant and pseudo-subordinate females under restricted conditions (Fig. 6A) returned towards shorter pre-treatment levels in the days following interaction. The return to shorter pre-interaction EODs suggests that elongated EODs are costly to maintain. There is evidence supporting this assertion: longer EODs are less efficient at precision time marking. As patterned EOD inter-pulse intervals encode information in time intervals, short-duration EODs should result in more accurate signaling (Kramer, 1990). In addition, increases in EOD duration correlate with increases in circulating androgen levels, and the maintenance of elevated androgen levels is known to be costly for many species. Androgens adversely impact immune systems and reduce survivorship by increasing metabolic costs (Grossman, 1985; Marler and Moore, 1988, 1989; Folstad and Carter, 1992). It is possible that the social signaling benefits associated with an elongated EOD outweigh the costs endured. EOD parameters may serve as condition-dependent indicators of the fish's resource holding potential. During free interactions, some subordinates that had shown no EOD duration increases during interaction exhibited post-treatment increases (Fig. 3A,B). The reasons for this opposite post-interaction response are not clear.
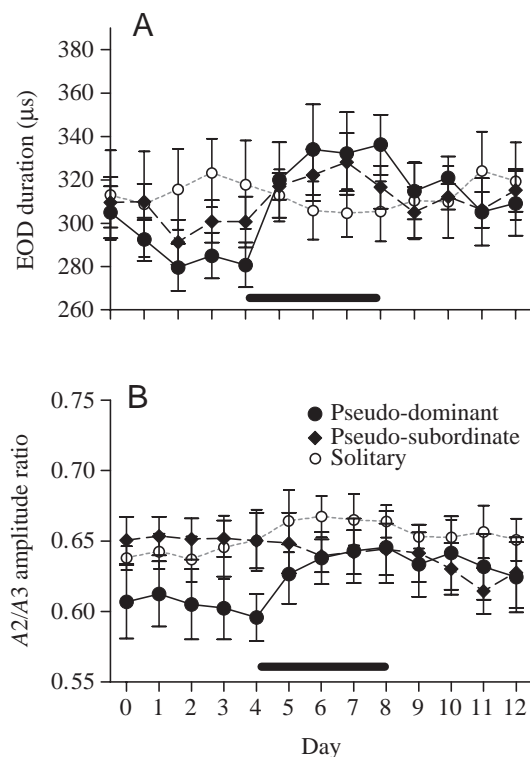

Fig. 6. Mean electric organ discharge (EOD) duration (A) and amplitude ratio (B) (error bars ± 1 S.E.M.; *N*=5 per group) as a function of pseudo-dominance status under conditions of restricted interaction (female *G. petersii* dyads). Pseudo-dominant females showed increases in EOD duration relative to their neighbors. Pseudo-subordinates showed no increase in amplitude ratio during the interaction period, although amplitude ratio did remain higher than or comparable with that of the pseudo-dominant group throughout the interaction. The horizontal bar spanning days 4–8 represents the duration of interaction.

Role of EOD amplitude in communication

The role of the EOD in mormyrid communication has mostly focused on differences in its temporal characteristics (Hopkins, 1981, 1986, 1999; Kramer, 1990). Little attention has been paid to the phase amplitude of the EOD (Bass, 1986). The socially mediated change in phase amplitude ratio shown here suggests a possible communicative function. Thus, in addition to EOD duration, the relative phase amplitude might serve as a cue to conspecifics about a neighbor's social status. The knollenorgan receptor pathway (mediating communication) is sensitive to temporal rather than amplitude differences (Hopkins and Bass, 1981; Hopkins, 1983, 1988, 1999; Bass and Hopkins, 1985; Zakon, 1986; Xu-Friedman and Hopkins, 1999). Are the observed changes in amplitude ratios a mere side effect or do these variations actually affect social communication?

The detection threshold for the individual phases of a single EOD will depend on their phase amplitudes. When the threshold for a transition between phases is reached, knollenorgans will produce a single spike for each detected EOD phase transition (Hopkins and Bass, 1981; Bell, 1986). We hypothesize that at a distance, within the signal's active space but below the detection threshold of one or more phases, a conspecific should detect the presence of an immature sender as being different from that of a socially dominant or sexually mature male. At the detection boundary of the signal's active space, signals with phases of different relative amplitude may be detected as monophasic, biphasic or triphasic. Thus, the higher $A2/A3$ ratio characteristic of the dominant fish in this experiment should, at a distance, be detected more often as biphasic rather than as monophasic.

At the boundary of the electro-communication range, where fish can first detect a potential mate or rival, the EODs broadcast by sexually mature and immature/subordinate individuals should differ in a simple quantitative way. Determining the number of discrete detectable phases may aid these fish in assessing dominance/sexual receptivity. A multiphasic EOD may also be less likely to attract electroreceptive predators (Stoddard, 1999). As a fish emits EODs in the context of defending its territory and/or attracting mates, it may also attract predators (specifically, the catfish *Clarias*). Multiple phases may allay the predation cost of increased signaling during agonistic or mating behavior by making the signal cryptic.

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